

JOURNAL OF BACTERIOLOGY

VOLUME 175 • NOVEMBER 1993 • NUMBER 22

Graham C. Walker, *Editor in Chief* (1996)
Massachusetts Institute of Technology,
Cambridge, Mass.

Terrance J. Beveridge, *Editor* (1997)
University of Guelph, Guelph, Canada

James G. Ferry, *Editor* (1996)
Virginia Polytechnic Institute and
State University, Blacksburg, Va.

Dan Fraenkel, *Editor* (1996)
Harvard Medical School, Boston, Mass.

Susan Gottesman, *Editor* (1994)
National Cancer Institute,
Bethesda, Md.

E. Peter Greenberg, *Editor* (1996)
University of Iowa, Iowa
City, Iowa

Carol A. Gross, *Editor* (1995)
University of Wisconsin,
Madison, Wis.

Dale Kaiser, *Minireview Editor* (1994)
Stanford University School of
Medicine, Stanford, Calif.

A. L. Sonenshein, *Editor* (1995)
Tufts University, Boston, Mass.

Kenneth N. Timmis, *Editor* (1997)
GBF, Braunschweig, Germany

Robert A. Weisberg, *Editor* (1995)
National Institute of Child
Health and Human
Development, Bethesda, Md.

EDITORIAL BOARD

Sankar Adhya (1993)
Michael Apicella (1995)
Stuart J. Austin (1993)
Barbara J. Bachmann (1993)
Douglas E. Berg (1994)
Robert W. Bernlohr (1994)
Volkmar Braun (1995)
Richard Calendar (1994)
George M. Carman (1994)
Sherwood Casjens (1994)
Trinidad Chakraborty (1994)
Wendy C. Champness (1994)
Mick Chandler (1993)
Nyles Charon (1995)
Keith F. Chater (1994)
Terrance G. Cooper (1993)
David L. Coplin (1995)
Donald Court (1994)
R. L. Crawford (1993)
John E. Cronan, Jr. (1995)
Jorge H. Crosa (1994)
Stanley J. Cryz, Jr. (1994)
Richard D'Ari (1994)
Dennis Dean (1995)
Victor de Lorenzo (1994)
Bruce Demple (1994)
Patrick P. Dennis (1993)
Miguel A. de Pedro (1993)
William D. Donachie (1994)
Timothy Donohue (1993)
Ron J. Doyle (1994)
Daniel Dykhuizen (1994)
S. Dusko Ehrlich (1994)
Rudolf Eichenlaub (1994)
Lindsay D. Eltis (1994)
Bert Ely (1994)
Wolfgang Epstein (1993)
Jeff Errington (1994)
Jorge Escalante-Semerena (1994)
David H. Figurski (1993)
Susan H. Fisher (1994)

Patricia L. Foster (1993)
Michael G. Fried (1994)
David I. Friedman (1995)
Bärbel Friedrich (1993)
Clement Furlong (1993)
Robert Gennis (1994)
Costa P. Georgopoulos (1993)
Jane Gibson (1994)
Larry Gold (1994)
Susan Golden (1994)
Richard L. Gourse (1994)
Nigel Grindley (1993)
Alan Grossman (1994)
Robert P. Gunsalus (1993)
William Haldenwang (1994)
Richard S. Hanson (1994)
Shigeaki Harayama (1993)
Caroline Harwood (1995)
Robert Haselkorn (1993)
Gerald L. Hazelbauer (1993)
George D. Hegeman (1994)
Roger Hendrix (1995)
Hauke Hennecke (1995)
C. F. Higgins (1993)
Joachim-Volker Holtje (1993)
Karin Ippen-Ihler (1993)
Edward E. Ishiguro (1994)
Klaus Jann (1995)
Gerald Johnston (1993)
Robert J. Kadner (1995)
Clarence I. Kado (1994)
Noel Keen (1994)
Patricia Kiley (1994)
H.-J. Knackmuss (1993)
Roberto Kolter (1994)
Wil N. Konings (1993)
Dennis J. Kopecko (1993)
Susan F. Koval (1994)
Terry Ann Krulwich (1993)
Carol Kumamoto (1993)
Harald Labischinski (1995)

Joseph Lam (1994)
Roger C. Levesque (1994)
Mary E. Lidstrom (1993)
Lasse Lindahl (1993)
John W. Little (1995)
Jack London (1993)
Sharon Long (1995)
Stephen Lory (1995)
Paul S. Lovett (1993)
Paul W. Ludden (1993)
Robert Macnab (1994)
Peter Maloney (1995)
Martin Marinus (1995)
Millicent Masters (1995)
Abdul Matin (1993)
Philip Matsumura (1995)
Russell Maurer (1993)
John Mekalanos (1994)
Paul Messner (1993)
Charles G. Miller (1994)
Virginia Miller (1994)
Shoji Mizushima (1994)
Charles P. Moran, Jr. (1994)
Edward A. Morgan (1993)
Gisela Mosig (1994)
Francis E. Nano (1994)
Dale Noel (1994)
Staffan Normark (1994)
Dennis Ohman (1994)
Gary Olsen (1994)
John S. Parkinson (1993)
Thomas R. Parr (1994)
Anthony Pugsley (1994)
Juan L. Ramos (1993)
Linda Randall (1993)
William Reznikoff (1995)
Gary P. Roberts (1993)
Jeffrey Roberts (1995)
Charles O. Rock (1993)
Lucia B. Rothman-Denes (1995)

Kenneth E. Rudd (1994)
H. Steven Seifert (1994)
Peter Setlow (1993)
Hideo Shinagawa (1994)
Howard A. Shuman (1994)
Michael Silverman (1995)
Gerald Smith (1994)
Issar Smith (1993)
G. Dennis Sprott (1995)
Catherine Squires (1993)
Gary Stacey (1994)
David Stahl (1993)
Brian Staskawicz (1993)
Robert Steffan (1993)
Michel Steinmetz (1994)
Valley Stewart (1994)
Susan C. Straley (1994)
Anne O. Summers (1993)
Robert Switzer (1993)
Andrew Taylor (1994)
Nancy Trun (1994)
Trevor R. Trust (1994)
Charles L. Turnbough, Jr. (1993)
Ronald Unterman (1994)
Mark Walker (1993)
Judy D. Wall (1993)
Barry Wanner (1993)
Chris M. Whitfield (1995)
William B. Whitman (1994)
David Wilson (1995)
Stephen C. Winans (1994)
Malcolm Winkler (1994)
C. L. Woldringh (1993)
Richard E. Wolf, Jr. (1995)
Hans Wolf-Watz (1994)
John L. Woolford (1994)
Henry C. Wu (1993)
Ryland Young (1993)
Takashi Yura (1994)
Howard Zalkin (1994)

Barbara H. Iglewski, *Chairman, Publications Board* **Linda M. Illig**, *Director, Journals*
Patrick N. Lacey, *Production Editor* **Catherine E. Blickendorfer**, *Assistant Production Editor*

The *Journal of Bacteriology*, a publication of the American Society for Microbiology (ASM), 1325 Massachusetts Ave., N.W., Washington, DC 20005-4171, is devoted to the advancement and dissemination of fundamental knowledge concerning bacteria and other microorganisms. Instructions to authors are published in the first issue each year; reprints are available from the editors and the Journals Division. The *Journal* is published twice monthly, one volume per year. The nonmember print subscription prices are \$360 (U.S.) (Canadians add 7% GST) and \$431 (other countries) per year; single copies are \$40 (Canadians add 7% GST). The member print subscription prices are \$79 (U.S.) (Canadians add 7% GST) and \$104 (other countries); single copies are \$10 (Canadians add 7% GST). For prices of CD-ROM versions, contact the Subscriptions Unit, ASM. Correspondence relating to subscriptions, defective copies, missing issues, and availability of back issues should be directed to the Subscriptions Unit, ASM; correspondence relating to reprint orders should be directed to the Reprint Order Unit, ASM; and correspondence relating to disposition of submitted manuscripts, proofs, and general editorial matters should be directed to the Journals Division, American Society for Microbiology, 1325 Massachusetts Ave., N.W., Washington, DC 20005-4171. Phone: (202) 737-3600.

Claims for missing issues from residents of the United States, Canada, and Mexico must be submitted within 3 months after publication of the issues; residents of all other countries must submit claims within 6 months of publication of the issues. Claims for issues missing because of failure to report an address change or for issues "missing from files" will not be allowed.

Second-class postage paid at Washington, DC 20005, and at additional mailing offices.

POSTMASTER: Send address changes to *Journal of Bacteriology*, ASM, 1325 Massachusetts Ave., N.W., Washington, DC 20005-4171.

Made in the United States of America. Printed on acid-free paper.

Copyright © 1993, American Society for Microbiology.
All Rights Reserved.

ISSN 0021-9193 CODEN: JOBAAY

The code at the top of the first page of an article in this journal indicates the copyright owner's consent that copies of the article may be made for personal use or for personal use of specific clients. This consent is given on the condition, however, that the copier pay the stated per-copy fee through the Copyright Clearance Center Inc., 27 Congress St., Salem, MA 01970, for copying beyond that permitted by Sections 107 and 108 of the U.S. Copyright Law. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale.

Author Index

- Ailion, Michael, 7200
 Akanuma, Hiroshi, 7138
 Aldovini, Anna, 7282
 Alix, Jean-Hervé, 7178
 Allen, S. H. George, 7348
 Alley, M. R. K., 7125
- Bannan, Jason D., 7228
 Barcak, Gerard J., 7269
 Bartlett, Douglas H., 7170
 Becker, Susanne, 7290
 Bensing, Barbara A., 7421
 Bingham, H., 7468
 Blanche, Francis, 7430
 Blumenthal, Robert M., 7160
 Bobik, Thomas A., 7200
 Boquet, Patrice, 7260
 Bowien, Botho, 7329
 Brabetz, Werner, 7488
 Bramanti, Thomas E., 7413
 Burdett, Vickers, 7209
- Cameron, Beatrice, 7430
 Cao, Yang, 7247, 7254
 Chan, V. L., 7468
 Chauhan, Sarita, 7222
 Chin, K., 7471
 Colbeau, Annette, 7404
 Crouzet, Joel, 7430
 Curran, Timothy M., 7189
 Cuyppers, Heinrich, 7236
- Debussche, Laurent, 7430
 Demple, Bruce, 7492
 Denninger, John W., 7160
 Dorocicz, Irene R., 7142
 Dunny, Gary M., 7421
- Eklund, Melvin W., 7260
 Elsen, Sylvie, 7404
 Eltis, Lindsay D., 7313
 Engel, Joanne, 7150
 Ennis, Don G., 7373
 Eriani, Gilbert, 7356
 Ernsting, Brian R., 7160
- Fall, Ray, 7216
 Farewell, Anne, 7170
 Friedman, Richard L., 7228
- Ganem, Don, 7150
 Ghigo, Jean-Marc, 7321
 Gibert, Maryse, 7260
 Girón, Jorge A., 7391
 Gottesman, M. E., 7471
 Götz, Friedrich, 7495
 Grant, Richard, 7150
 Greenberg, E. P., 7307
 Grundy, Frank J., 7348
- Hani, E., 7468
 Happe, Birgitta, 7313
 Hauser, Daniel, 7260
 Hedderich, Reiner, 7313
 Heidelberg, Michael, 7479
 Henkin, Tina M., 7348
 Henrich, Bernhard, 7290
 Hidalgo, Elena, 7492
 Hiramatsu, Keiichi, 7483
 Ho, Alice Suk Yue, 7391
 Holt, Stanley C., 7413
 Husson, Robert N., 7282
- Jimenez, Antonio, 7474
- Kaiser, Dale, 7450
 Kim, N. W., 7468
 Klein, Russell, 7150
 Kogoma, Tokio, 7247, 7254
 Kolibachuk, Dana, 7307
 Krebes, Kathleen, 7363
 Kulthanan, Kanokvalai, 7483
 Kusian, Bernhard, 7329
- Lacalle, Rosa A., 7474
 Létoffé, Sylvie, 7321
 Li, Ziyi, 7492
 Liebi, Wolfgang, 7488
 Lin, H. C., 7383
 Little, John W., 7373
 Liu, Ju, 7441
- Lombardi, R., 7468
 Lory, Stephen, 7463
 Losick, Richard, 7341
 Louie, H., 7468
 Lu, Hong-Mei, 7463
- MacInnes, Janet I., 7228
 Madan, Anuradha P., 7301
 Maddock, Janine R., 7125
 Magasanik, Boris, 7441
 Malumbres, Marcos, 7356
 Martin, Franck, 7356
 Martín, Juan F., 7356
 Mateos, Luis M., 7356
 Matthews, Rowena G., 7160
 McNally, Catherine, 7363
 Mizuno, Hideaki, 7138
 Mizushima, Shoji, 7463
 Moran, Michael J., 7228
 Mount, David W., 7373, 7505
- Neidhardt, Frederick C., 7170
 Nemecek-Marshall, Michele, 7216
 Neshat, Shadi, 7363
 Ng, D., 7468
 Nierzwicki-Bauer, Sandra A., 7301
 Nunoshiba, Tatsuo, 7492
- O'Brian, Mark R., 7222
 Oguiza, José A., 7356
 Ohta, Hisako, 7483
 Oke, Valerie, 7341
- Peterson, Kenneth R., 7505
 Pi, Jing, 7500
 Pisabarro, Agustín, 7356
 Pittard, A. J., 7500
 Plapp, Roland, 7290
 Plumbridge, Jacqueline A., 7178
 Poole, Keith, 7363
 Popoff, Michel R., 7260
 Poth, Harald, 7313
- Redfield, Rosemary J., 7142
 Richaud, Pierre, 7404
 Roth, John R., 7200
 Rowland, Raymond R. R., 7247
 Ruggles, James A., 7216
 Rustchenko, Elena P., 7189
- Schäferjohann, Jens, 7329
 Schairer, Hans Ulrich, 7479
 Schleifer, Karl-Heinz, 7488
 Schoolnik, Gary K., 7391
 Schroeder, Ulrich, 7290
 Shapiro, Lucille, 7125
 Shean, C. S., 7471
 Sherman, Fred, 7189
 Shiga, Yasuhiro, 7130
 Shiga, Yoko, 7138
 Skladny, Heyko, 7479
 Soltes, Glenn A., 7228
- Tan, Ming, 7150
 Tercero, Jose A., 7474
 Thibaut, Denis, 7430
 Thöny-Meyer, Linda, 7450
 Timmis, Kenneth N., 7313
- Udaka, Shigezo, 7130
- Vanet, Anne, 7178
 Vara, Jesus, 7474
 Vignais, Paulette M., 7404
- Wada, Akihito, 7483
 Wandersman, Cécile, 7321
 Waters, Debra A., 7348
 Welch, Timothy J., 7170
 Williams, Pascale M., 7142
 Witke, Claudia, 7495
 Wittman, Vaughan, 7383
 Wong, H. C., 7383
 Wookey, Peter J., 7500
- Yamagata, Hideo, 7130
 Yoo, Je-Geun, 7329
 Young, Richard A., 7282
- Zulty, James J., 7269
 Zumft, Walter G., 7236

UPCOMING MINIREVIEWS

Transcription Repair Coupling and Mutation Frequency Decline by
 Christopher P. Selby and Aziz Sancar

*Color Sensing in the Archaea: a Eukaryotic-Like Receptor Coupled to
 a Prokaryotic Transducer* by John L. Spudich

*The Winds of (Evolutionary) Change: Breathing New Life into
 Microbiology* by Gary J. Olsen and Carl R. Woese

*Quorum Sensing in Bacteria: the LuxR/LuxI Family of Cell
 Density-Responsive Transcriptional Activators* by W. Claiborne
 Fuqua, Stephen C. Winans, and E. Peter Greenberg

1325 Massachusetts Ave. NW • Washington, DC 20005-4171 • (202) 942-9319 • FAX (202) 942-9347

Initiation Memberships are initiated and renewed in January each year. **Unless there are directions to the contrary**, membership nominations received prior to September 1 are credited to the current year. **Nominations received after September 1 will become effective the following January.**

NAME MISS
MS.
MRS. MR. FIRST INITIAL LAST
(CIRCLE ONE) MAIL NAME AS YOU WANT IT TO APPEAR ON YOUR MAILING LABEL
ADDRESS WHERE YOU WANT TO RECEIVE YOUR SUBSCRIPTIONS

STATE/PROVINCE ZIP/POSTAL CODE COUNTRY
PHONE () FAX () YEAR OF BIRTH SEX
HIGHEST DEGREE MAJOR FIELD OF STUDY
SCHOOL
SIGNATURE OF APPLICANT DATE
SIGNATURE OF CHAIRMAN
OF MAJOR DEPARTMENT MEMBER # | | | | | | | |
*NOMINATED BY MEMBER # | | | | | | | |
SIGNATURE OF ASM MEMBER

*If your departmental chairman is a member of the ASM, a nominating signature is not required. If you are not associated with an ASM nominating member, you can still send in this member application form and we will contact you. Be sure to include your dues.

How did you first learn about the ASM? (Check one):

- ☐ A colleague ☐ An ASM journal ☐ Presenting a paper at an ASM meeting
☐ A professor ☐ An ASM Branch ☐ An advertisement in ASM journal ☐ Direct mail inquiry

Please check:

- ☐ Enclosed is my dues payment **(U.S. Dollars only)** **\$15**
- ☐ Please send me the following ASM journal(s) at Member Price(s):

	Canada	Print Only	Amount*
Antimicrobial Agents & Chemotherapy		\$52	_____
Applied & Environmental Microbiology		\$53	_____
Molecular & Cellular Biology		\$86	_____
Clinical Microbiology Reviews		\$21	_____
Infection & Immunity		\$55	_____
Int'l Journal of Systematic Bact.		\$37	_____
Journal of Bacteriology		\$85	_____
Journal of Clinical Microbiology		\$52	_____
Journal of Virology		\$87	_____
Microbiological Reviews		\$27	_____
Clinical & Diagnostic Laboratory Immunology		\$43	_____
ASM News		\$0	_____

Total Journal Fees \$

*7% GST has been included in the subscription price

Add your \$15 Membership Dues +15

Total \$ _____

A membership card, division registration form, and the journal(s) of your choice will be sent within 90 days upon completion of processing. ASM dues are tax deductible to the extent permitted by law. ASM designates \$12 of your dues for ASM News. **Rates are for 1994 only.**

Applicants **must** remit in U.S. Dollars by check or draft payable to ASM through a U.S. bank located within the Continental U.S. Applicants from Canada may use check made out in U.S. Dollars and drawn on a Canadian bank or applicants may choose to pay with VISA, MasterCard, Eurocard, or American Express. If that is your preference, please fill in the box below.

☐ VISA # _____
☐ MASTERCARD # _____
☐ AMEX # _____
☐ EUROCARD # _____
 TODAY'S DATE _____ SIGNATURE _____
 MONTH DAY YEAR NAME AS IT APPEARS ON YOUR CREDIT CARD
 SIGNATURE _____

1994 APPLICATION FOR FULL MEMBERSHIP IN THE AMERICAN SOCIETY FOR MICROBIOLOGY

1325 Massachusetts Ave. NW • Washington, DC 20005-4171 • (202) 942-9319 • FAX (202) 942-9347

Eligibility ASM welcomes to full membership anyone who is interested in its objectives and has a minimum of a bachelor's degree or equivalent in microbiology or a related field.

Initiation Memberships are initiated and renewed in January each year. **Unless there are directions to the contrary**, membership nominations received prior to September 1 are credited to the current year. **Nominations received after September 1 will become effective the following January.**

NAME ^{MISS DR.} ^{MS.} ^{MRS. MR.} FIRST INITIAL LAST
(CIRCLE ONE) MAIL NAME AS YOU WANT IT TO APPEAR ON YOUR MAILING LABEL
ADDRESS WHERE YOU WANT TO RECEIVE YOUR SUBSCRIPTIONS
STATE/PROVINCE ZIP/POSTAL CODE COUNTRY
PHONE () FAX () YEAR OF BIRTH SEX
HIGHEST DEGREE SUBJECT AREA YEAR EARNED
EMPLOYER PRESENT POSITION
SIGNATURE OF APPLICANT DATE
*NOMINATED BY SIGNATURE OF ASM MEMBER MEMBER #

*If you are not associated with an ASM nominating member, you can still apply for membership and we will contact you if there is a problem

Member Information How did you first learn about the ASM? (Check one):
☐ A colleague ☐ An ASM journal ☐ An ASM Branch ☐ Direct mail inquiry
☐ A professor ☐ A workshop, conference or meeting ☐ An advertisement in ASM journal

Dues Annual dues for 1994 are \$75. Dues include ASM News (monthly) and a \$51 credit which may be deducted from the total cost of the journal(s) you purchase at the special membership rates indicated below.

Journals ☐ Enclosed is my dues payment (U.S. Dollars only) \$75
☐ Please send me the following ASM journal(s) at Member Price(s):

For CD-ROM select: DOS <input type="checkbox"/> MAC <input type="checkbox"/>	Canada	Print Only	CD-ROM Only	Print & CD-ROM	Amount*
Antimicrobial Agents & Chemotherapy		\$52	\$162	\$186	
Applied & Environmental Microbiology		\$53	\$163	\$187	
Molecular & Cellular Biology		\$86	\$166	\$214	
Clinical Microbiology Reviews		\$21	\$80	\$91	
Infection & Immunity		\$55	\$164	\$188	
Int'l Journal of Systematic Bact.		\$37	\$81	\$102	
Journal of Bacteriology		\$85	\$165	\$213	
Journal of Clinical Microbiology		\$52	\$160	\$186	
Journal of Virology		\$87	\$167	\$215	
Microbiological Reviews		\$27	\$84	\$94	
Clinical & Diagnostic Laboratory Immunology		\$43	\$128	\$144	
ASM News		\$0	N/A	N/A	

AA
AE
CB
CM
IA
IJ
JB
JC
JV
MR
LI

Total Journal Fees \$

*7% GST has been included in the subscription price

Subtract your \$51 Member Journals Credit - \$51

Subtotal (if less than zero, enter zero) \$

Add your \$75 Membership Dues + 75

Total (Dues plus Journals). If total is less than \$75.00, enter \$75 \$

PAYMENT IN U.S. DOLLARS MUST ACCOMPANY APPLICATION

A membership card, voting division form, ASM Placement Service Information and the journal(s) of your choice will be sent within 90 days upon completion of processing. ASM dues are tax deductible to the extent permitted by law. ASM designates \$13 of your dues for ASM News. **Rates are for 1994 only.**

Applicants **must** remit in U.S. Dollars by check or draft payable to ASM through a U.S. bank located within the Continental U.S. Applicants from Canada may use check made out in U.S. Dollars and drawn on a Canadian bank or applicants may choose to pay with VISA, MasterCard, Eurocard, or American Express. If that is your preference, please fill in the box below.

☐ VISA # ☐ MASTERCARD # ☐ AMEX # ☐ EUROCARD #
TODAY'S DATE MONTH DAY YEAR NAME NAME AS IT APPEARS ON YOUR CREDIT CARD
SIGNATURE EXPIRATION DATE MO YR